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SOIL FAUNA AND SITE ASSESSMENT IN BEECH STANDS OF THE BELGIAN ARDENNES

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Abstract: Soil fauna (macrofauna and mesofauna) were sampled in thirteen beech forest stands of the Ardenne mountains (Belgium) covering a wide range of acidic humus forms. The composition of soil fauna was well-correlated not only with humus form, but also with elevation, phytosociological type, tree growth, mineral content of leaf litter and a few soil parameters such as pH and C/N ratio. The nature of mechanisms which can explain these relationships is discussed under the light of existing knowledge.

Résumé: La faune du sol (macrofaune et mésofaune) a été échantillonnée dans treize peuplements de hêtre des Ardennes belges, couvrant une gamme étendue de formes d'humus acides. La composition faunistique est bien corrélée, non seulement avec la forme d'humus, mais aussi avec l'altitude, le groupement phytosociologique, la croissance des arbres, la composition minérale de la litière de feuilles et quelques paramètres édaphiques tels que le pH et le rapport C/N. La nature des mécanismes pouvant expliquer ces relations est discutée, à la lueur des connaissances actuelles.

Introduction

The assessment of site quality for the growth of forest stands has been based mainly on ground vegetation (Rodenkirchen 1985) and soil features (Turvey and Smethurst 1985). When the soil type does not change heavily, it has been observed that strong discrepancies in forest productivity may be explained by the rate at which litter disappears from the ground surface (Delecour 1978). This rate, expressed by a coefficient calculated first by Jenny et al. (1949), was proposed as a site factor for European beech (*Fagus sylvatica* L.) forests by Delecour and Weissen (1981).

The disappearance of canopy litter from the ground surface (improperly called decomposition) is strongly associated to humus form, i.e. moder and moreover mor humus are characterized by a slower rate of disappearance of leaf litter than mull humus (Van der Drift 1963). This phenomenon has been found to result from the consumption of litter by fauna and microflora, which vary in quantity and quality from a site to another (Toutain 1987; Schaefer and Schauer mann 1990; Muys and Lust 1992).

We contrasted soil macro- and mesofauna with other site factors in 13 beech forests of the Belgian Ardennes, which share the same parent rock and regional climate but strongly differ by their productivity and humus form. In a previous paper (David et al. 1993) we characterized mull humus by a higher diversity of macrofaunal groups when compared to moder humus. Nevertheless the discriminative power of macrofauna was poor in the moder group (from hemimoder to dysmoder), where elaterid larvae (Insecta, Coleoptera) were one of the few macrofaunal taxa present. We hypothesized that a more complete study of soil fauna could allow to better discriminate these sites.

Study sites

The sites were thirteen beech (*Fagus sylvatica*) forest stands made of full-grown trees, where soils and plant communities had been previously studied in relation with forest productivity (Manil et al. 1953, 1963; Dagnelie 1956a, 1956b, 1957). They are typical of the forest cover of the Ardenne mountains. The climate shares atlantic and mountain features, being characterized by abrupt changes in temperature, with a mean annual temperature of 7.2°C and a mean annual rainfall ranging from 1000 to 1400 mm according to geographical location. These old Hercynian mountains have been strongly eroded, culminating at 694 m altitude. Rocks, ranging from Cambrian to Devonian age, are poor in bases (schists, graywackes, quartzites). Phytosociological and soil types are given in Table 1, together with elevation and geographical location.

Material and methods

Soil fauna

Macrofauna was sampled by forcing a 30x30 cm steel frame into the litter sensu lato and the first 5 cm of underlying soil. Three samples were taken in each site in June 1989, then three others in October 1989. Samples were placed in plastic bags then transported to the laboratory. Animals were extracted

within 15 days by the dry-funnel method. For soil-dwelling earthworms an additional sampling around the same plots was done by watering a 50x50 cm area three times at 10' intervals with diluted formaldehyde as a repellent (2, 3 then 4‰ v/v), then digging the soil underneath down to 30 cm.

Mesofauna was sampled by forcing a 5 cm diameter steel cylinder into the top 15 cm of soil (litter included), at the same dates as for macrofauna, but with only 2x2 replicates. Samples were then processed as abovementioned.

Given the poor efficiency of the dry-funnel method for enchytraeid worms, these animals, together with other visible soil animals, were hand-sorted directly in special soil cores (5x5x15 cm) which were taken in June 1989 for micromorphological purposes (2 replicates in each site), according to the method described by Ponge (1991). Hand-sorting was performed by dividing the cores into small volumes of litter and soil which were observed into ethyl alcohol under a dissecting microscope. Plant fragments as well as soil aggregates were thoroughly comminuted and all mesofauna and macrofauna were recovered, thus allowing comparisons with extraction methods.

Table 2 indicates the animal groups which were identified and counted, together with the methods used for their recovery.

Litter accumulation

The surface weight of litter layers, estimated just after main leaf fall, was used to compare the different sites. The O horizon, i.e. the pure or near pure organic matter accumulated at the top of the soil profile (Delecour 1980; Brêthes et al. 1995; Jabiol et al. 1995) can be divided into several horizons called OL (entire leaves), OF (fragmented leaves) and OH (holorganic faecal material). These horizons are called L, F, and H, respectively, in the classification of Green et al. (1993), which assigns the term O horizon to wetland soils, only. The more rapid is the disappearance of litter from the ground, the less important are OF and OH horizons compared to OL horizon, which at the end of autumn is mainly made of freshly fallen litter. We calculated the litter accumulation index (LAI) as the ratio W_{OF+OH}/W_{OL} , where W_{OF+OH} and W_{OL} are the areal weights of OF+OH and OL horizons, respectively. For that purpose, these horizons were sampled in the study sites at the end of November 1989, by forcing six 15 cm

diameter stainless steel cylinders through the topsoil. Samples were transported to the laboratory then dried in air-forced chambers at constant temperature (25°C) during a fortnight, before being weighed to the nearest 10⁻²g. After this step, beech leaves were sorted and weighed separately, in the OL horizon only.

Stand productivity

Following previous work on the same sites (Dagnelie 1956a, 1956b, 1957), a linear relationship was demonstrated between the mean total height of co-dominant trees and the mean annual increment of wood available for timber production. For instance total heights of 25, 30, and 35 m were associated with increments of 3.6, 5.4, and 7.4 m³.ha⁻¹.yr⁻¹, respectively. Thus we used total height of adult co-dominant trees as a productivity index. This height was measured on six co-dominant trees growing in the vicinity of the sampling plot. In some cases (sites 1, 5, 100) a lower number of individuals (3, 3, 2, respectively) was used, due to the smaller size of the study site or timber harvesting during previous years. The total height of each selected tree was measured with a Suunto Hypsometer® compass to the nearest ¼m.

Litter chemical analyses

Beech leaf litter and miscellaneous litter were separately analysed in the OL samples used for the determination of the litter accumulation index. For that purpose samples from the same site were bulked into a composite sample which was ground then dried overnight at 103°C, in order to determine its dry mass. The ash content was measured by calcinating 1g of powdered dry litter in a muffle furnace at 550°C for 5h. Total nitrogen was quantified by Kjeldahl digestion into a Kjelttec® autoanalyser on a separate 200 mg sub-sample. Total carbon was quantified by the Anstett method, using concentrated sulfuric acid and potassium bichromate as oxydants and Mohr salts for titration, on a 100 mg sub-sample. Other elements (Ca, Mg, K, P, Fe) were determined by high frequency plasma emission photometry on the ashed sub-sample after dissolution in hydrochloric acid and elimination of silica by hydrofluoric acid.

Humus form

1

2 Humus form was identified in each sampling plot in June 1989 while taking samples for
3 micromorphological studies (two replicates in each site). Nomenclature was derived from Brêthes et al.
4 (1995). According to this classification the O horizon (litter sensu lato) and the A horizon (organo-
5 mineral horizon underlying the O horizon) may vary somewhat independantly, transition forms between
6 mull and moder groups being called hemimoder (belonging to the moder group), amphemull and
7 dysmull (belonging to the mull group) according to the absence or presence of a crumbly structure in
8 the A horizon, combined with absence or presence of an OH horizon.

9

10 **Soil chemical analyses**

11

12 These analyses were performed separately on 6 replicate samples taken in each site after collection of
13 the O horizon as abovementioned. The underlying A horizon was collected down to 5 cm depth under
14 the bottom of the O horizon, then air-dried until analysis. Samples were sieved (<2 mm) then
15 homogenized. Water pH and potassium chloride pH were measured on a 5g sub-sample diluted with
16 deionized water (soil:water 1:1 w/w). A 50g sub-sample was crushed with pestle and mortar, then
17 sieved (<200 µm) for further analyses. Cation exchange capacity was measured on a 10g sub-sample
18 by percolating the soil with 1N calcium chloride until saturation of exchange sites then displacing
19 calcium with 1N potassium nitrate. Determination of calcium and chloride content was performed in the
20 filtrate by flame nitrous oxyde-acetylene atomic absorption photometry, and complexometry with a
21 Technicon® autoanalyser, respectively. Exchangeable cations (Ca, Mg, K, Na) were determined on a
22 10g sub-sample after displacement of sorbed cations with ammonium nitrate. Potassium and sodium
23 were determined on the filtrate by flame emission photometry, calcium and magnesium by flame
24 atomic absorption photometry. Total carbon and nitrogen were determined with a CHN Carlo Erba®
25 analyser on a 5mg sub-sample. Total bases (Ca, Mg, K, Na), iron and manganese were determined on
26 1g sub-sample after boiling with concentrated hydrochloric acid. Potassium and sodium were
27 determined by flame air-acetylene emission photometry, magnesium, iron and manganese by flame
28 air-acetylene atomic absorption photometry, and calcium by flame nitrous oxyde-acetylene atomic
29 absorption photometry. Total phosphorus was determined on a 1g sub-sample with a Techicon®
30 autoanalyser after treatment with concentrated hydrogen peroxyde followed by boiling with perchloric
31 acid.

Data analysis

Effects of season or extraction methods on animal densities were tested by means of two-way ANOVA using sites as blocks (Sokal and Rohlf 1995; Rohlf and Sokal 1995). In order to ensure additivity of variance data were previously transformed into $\log(x+1)$. All means given for each site were calculated using log-transformed data.

Sites were ordinated according to their faunal composition by help of correspondence analysis (Greenacre 1984). Active variates were mean densities of the different animal groups in the 13 studied sites. Data were reweighted to a unit standard deviation and focused around a mean of 10 by using the transformation $x \rightarrow (x-m)/s+10$, where m is the mean and s is the standard deviation for each variate, respectively. By this way the different animal groups have a similar mass and similar total variance, thus allowing factorial coordinates to be directly interpreted in terms of their contribution to factorial axes. Each variate was associated with a conjugate, varying in an opposite sense ($x'=20-x$). Thus each animal group will be represented by two points, one indicating higher densities for this group, the other lower densities. Passive variates, describing environmental conditions, were added, in order to measure their degree of relationship with this ordination, which was based on faunal composition only. Passive data were reweighted and focused in a similar way. Correlation coefficients between factorial axes and variates or between variates were calculated on transformed data according to the product-moment formula of Pearson and were tested by the t-test method (Sokal and Rohlf 1995).

Results

Choice of methods for recovering animals

Most macrofaunal groups were sampled on a much wider surface than mesofauna, given lower density and patchiness of these animals in the soil (Macfadyen 1957). Enchytraeid worms were recovered by dissecting litter and humus samples at a high magnification. This was also the case for copepods,

phthiracarid mites, miscellaneous mites, pauropods, Symphyla, Protura, cecidomyid, ceratopogonid, chironomid, sciarid, miscellaneous fly larvae, cochineals, and booklice. In all these cases the advantage of direct counting against active extraction of animals was evident, thus we judged preferable to chose the first method, despite the poorer number of replicates (2, against 4 for active extraction of mesofauna). For miscellaneous oribatid mites and springtails, which were collected in high numbers both by dry funnels and by direct counting, an ANOVA was performed on June samples (2 replicates for each method in each of the 13 sites). Extraction by the dry-funnel method furnished more animals than direct counting for oribatid mites ($p < 0.0001$), but differences between methods were insignificant for springtails ($p = 0.17$). The methods chosen for the different animal groups are indicated in Table 2.

Seasonal influences

Densities of three macrofaunal groups were significantly affected by season, with more animals in November than in June, i.e. spiders, adult beetles, and pseudoscorpions, with $p = 0.003$, 0.03 , and $p < 0.0001$, respectively (two-way ANOVA). Only two mesofaunal groups were significantly affected, with more animals in June than in November, i.e. springtails and miscellaneous oribatid mites, with $p = 0.006$ and 0.01 , respectively. Given that significant differences were few, we decided to pool the data from the two sampling periods into a composite mean for each study site.

Ordination of sites according to faunal composition

Correspondence analysis of faunal data helped to ordinate sites according to their faunal composition. The first axis extracted 25% of the total variance. Examination of the position of sites and zoological groups along this axis (Fig. 1) and of faunal densities (Table 3) showed a progressive shift from macrofauna-dominated to enchytraeid-dominated sites, with the exception of some macrofaunal groups such as click-beetle larvae (CLIC), Diplura (DIPL) and cochineals (COCH). On the positive side of axis 1 only enchytraeid (ENCH) and click-beetle (CLIC) densities were significantly correlated with axis 1 coordinates. On the negative side limnobiid larvae (LIMN), scatopsid larvae (SCAT), dolichopodid-empidid larvae (DOEM), milliped (MILL), Trichoptera larvae (TRIC), cantharid larvae (CANT), woodlice (ISOP), earthworm (LUMB), pseudoscorpion (PSEU), rhagionid larvae (RHAG),

chironomid larvae (CHIR), mollusc (MOLL), and muscid larvae (FANN) densities, were all significantly correlated with axis 1 coordinates. All these groups were significantly correlated between them, indicating that the global trend depicted by axis 1 was a community gradient.

We may nevertheless question whether groups placed in an intermediate position, i.e. not far from the origin, i) do not vary to a great extent between sites, ii) are influenced by other factors than this community gradient, or iii) are more abundant in sites placed in an intermediary position (such as sites 3, 17, 22, 24) than in sites placed far from the origin on the positive or on the negative side of axis 1. The case of groups such as ants (ANTS), copepods (COPE), earwigs (DERM), miscellaneous insect larvae (LMIS), psychodid larvae (PSYC), and booklice (PSOC) cannot be accounted for, since they are scarce and present in a low number of sites. On the contrary, oribatid mites (ORIB) and sciarid larvae (SCIA), placed not far from the origin, are abundant and present everywhere. The first group proved to be significantly more abundant in some sites than in others ($F = 3.56$, d.f. = 12/39, $p = 0.0013$), the second group did not significantly differ between sites ($F = 1.17$, d.f. = 12/13, $p = 0.39$). Examination of the mean densities of Oribatid mites in the 13 sites (Table 3) showed that these animals were very abundant in sites located on both sides of axis 1. Thus their distribution did not follow the global trend exhibited by the first axis of correspondence analysis (case ii). Sciarid larvae were rather evenly distributed (case i). We did not register the third postulated case, i.e. zoological groups characteristic of sites placed in an intermediary position by the analysis.

Explanatory value of site features

Elevation, together with phytosociological type and humus form, proved to discriminate the studied sites, ordinated according to axis 1 of correspondence analysis (Fig. 2, Table 4). Elevation was significantly and positively correlated with axis 1 ($r = 0.65$, $p < 0.05$), thus increasing from site 100 to site 4. Along this community gradient humus form varied from dysmull to dysmoder, i.e. from rapid to slow disappearance of litter (Brêthes et al. 1995). Oligomull was undistinguishable from dysmull, and amphimull, hemimoder and eumoder were placed in an intermediary position, being undistinguishable from each other. The phytosociological type varied from *Melico-Fagetum festucetosum*, with a rich ground flora and highly productive, which is characteristic of lowland sites (Thill et al. 1988), to *Luzulo-Fagetum vaccinietosum*, much poorer in ground flora and weakly productive, which is mostly

established on tablelands and sunny slopes. Soil types did not express a good relationship with axis 1, contrary to humus forms and phytosociological types.

Total height of co-dominant trees was significantly correlated with axis 1 ($r = -0.56$, $p < 0.05$), together with pH H₂O ($r = -0.75$, $p < 0.01$), pH KCl ($r = -0.71$, $p < 0.01$), and C/N ratio of the A horizon ($r = 0.88$, $p < 0.01$). Thus the community gradient from site 100 to site 4 was characterized by a bulk decrease in the height of trees and soil pH, and an increase in C/N ratio (Fig. 3, Table 4). No significant correlation was found for axis 1 with the litter accumulation index (LAI) and surface weight of OF+OH horizons.

Among total soil elements, only manganese was significantly correlated with axis 1 ($r = -0.87$, $p < 0.01$), its content in the top 5 cm of the A horizon decreasing from site 100 to site 4 (Fig. 4, Table 4). No significant correlation was found with cation exchange capacity nor exchangeable bases.

The richness of litter in mineral matter (ash content) was significantly correlated with axis 1, both for total litter and beech leaf litter ($r = -0.86$, $p < 0.01$ and $r = -0.77$, $p < 0.01$, respectively), decreasing from site 100 to site 4 (Fig. 5, Table 4). At the elemental scale the same trend was depicted by iron, calcium and magnesium, both for total litter and beech leaf litter.

Discussion

The fauna of investigated sites was clearly varying in the same sense as soil fertility, this feature being expressed not only by pH and C/N ratio of the A horizon (Brady 1984), but also by mineral richness of leaf litter (Mangenot and Toutain 1980) and tree growth (Dagnelie 1957). We may nevertheless ask to which extent the faunal composition was here determined by site conditions. The possibility of feedback loops between fauna and site conditions should not be overlooked, too, except for some features such as elevation which are not placed under biological control.

In the Belgian Ardennes, altitude has been locally considered as the most prominent regional factor influencing stand productivity, humus and phytosociological type (Dagnelie 1957; Manil et al. 1963; Delecour and Prince-Agbodjan 1975; Thill et al. 1988). Higher altitude means colder climate and higher precipitation, in a geographic zone (the Ardenne mountains) where the regional climate is harsher and more rainy than in any other part of Belgium (average annual temperature 7°C, average annual rainfall 1100 mm). This may have consequences on the level of biological activity, but also on the leaching of mineral elements during periods of low biological activity (winter), upland sites being thus impoverished compared to lowland sites. In addition, erosion progressively enriched lowland sites in nutrients at the expense of upland sites (Duchaufour 1995). Combined to climate effects of altitude (Manil et al. 1963), higher elevation (upland sites) means also harder parent rocks than along slopes (Thill et al. 1988) and even more than along rivers (lowland sites, the more typical being site 100, located along the river Masblette). This geomorphological effect of altitude may affect the cycling of nutrients through differences in mineral weathering (Gaiffe and Bruckert 1990). Due to synergistic effects of climate, erosion and rock hardness, upland sites will be thus characterized by poorer availability of mineral elements for organisms, when compared to lowland sites.

In the litter compartment of the beech ecosystem, the availability of elements to litter-consuming animals is related to mineral richness of beech and total litter, sites with a mull fauna (negative side of axis 1) having richer beech and total litter than sites with a moder fauna (positive side of axis 1). It should be highlighted that this effect of litter richness concerns more metals (iron) and alkaline earths (calcium, magnesium) than main nutrients such as nitrogen, potassium, and phosphorus, or the C/N ratio, contrary to literature data on plant litter decomposition (Melillo et al. 1982) and palatability of leaf litter to saprophagous animals (Hendriksen 1990). The high calcium requirements of most earthworm (Pearce 1972), milliped (Reichle et al. 1969; Carter and Cragg 1976) and woodlice (Krivolutzky and Pokarzhevsky 1977) species, all typical of the negative side of axis 1 (mull side) may nevertheless explain the absence of these groups in sites with a poorer Ca content of litter (moder side). But here possible feed-back loop effects, which reinforce this selective process, must be considered, i) through the cycling of mineral elements by fauna, ii) through the phenolic content of beech foliage. Woodlice, millipeds and earthworms have been consistently demonstrated to increase the leaching of nutrients from decaying leaf litter (Anderson et al. 1983; Morgan et al. 1989), thus increasing their availability to plants (Haimi and Einbork 1992). Sulkava et al. (1996) demonstrated that at low to medium moisture

the structure of soil animal communities determined the extent of N mineralization. Thus the availability of mineral elements for vegetation may be increased or decreased according to composition of the soil fauna (Scheu and Parkinson 1994). This in turn may affect the mineral composition of the beech foliage (Toutain and Duchaufour 1970). The phenolic content of tree foliage has been demonstrated to influence the palatability of leaves to earthworms (Satchell and Lowe 1967), a lower content in phenolics being associated with higher palatability. Thus the phenolic content of litter may affect directly some animal groups through their food preferences. It also determines soil-forming and microbial processes, a higher phenolic content of tree foliage and litter increasing the leaching of bases during periods of low biological activity and making proteins harder to decay through complexing processes (Davies 1971). Conversely the production of phenolics and other secondary plant metabolites increases in nutrient-poor conditions (Kuiters 1990), thus self-reinforcing the process.

We can now examine the influence of soil chemistry and humus form on soil animals, and its counterpart, their influence on these conditions. Observations on the distribution of soil animals in varying site conditions proved that, beside considerable variation from species to species, some zoological groups in bulk are seemingly correlated with soil and humus properties. Less acid soils, with mull humus forms, were found to be characterized by a richer and more abundant saprophagous macrofauna, especially earthworms, molluscs, woodlice and millipeds (Bornebusch 1930; Van der Drift 1962; Abrahamsen 1972b; Petersen and Luxton 1982; David 1987; Herlitzius 1987; Staaf 1987; Schaefer and Schauer mann 1990; Schaefer 1991; Ponge and Delhaye 1995), like in the present study. The abovementioned association of chironomid fly larvae with mull humus (negative side of axis 1) has been already registered by Healey and Russel-Smith (1971). The association of Nematocera fly larvae families (Rhagionidae, Dolichopodidae, Empididae, Chironomidae, as representative in our samples) with less acid soils has been already established by Herlitzius (1987). In the case of enchytraeids, literature data indicate that species richness decreases when acidity increases and unincorporated organic matter accumulates (moder or mor humus), the opposite trend being observed with total abundance, due to dominance of *Cognettia sphagnetorum* in raw humus (Abrahamsen 1972a; Healy 1980; Petersen and Luxton 1982), thus confirming our results on this group as a whole. A similar phenomenon has been observed by Bornebusch (1930) on click-beetle (Elateridae) larvae in beech forests of Denmark, the density of *Athous subfuscus* increasing dramatically in raw humus (in fact dysmoder), which is confirmed by our observations on beech forests in Belgium (David et al. 1993).

1

2 The direct action of soil chemistry on soil animals is difficult to evidence, due to multiple
3 interactions with trophic and habitat features, although it has been suspected following community
4 studies (Ponge 1993; Healy 1980), and studies on the sensitivity of animals to acidity and osmolarity of
5 soil solutions (Laverack 1961; Jaeger and Eisenbeis 1984; Heungens and Van Daele 1984).
6 Experimental liming has been found detrimental to enchytraeid species living in acid conditions
7 (Abrahamsen 1983; Huhta et al. 1986), the contrary being true for earthworms (Huhta 1979; Toutain et
8 al. 1987; Robinson et al. 1992). These results should nevertheless be accepted with caution, because
9 in the short term abrupt changes in soil conditions following lime (or acid) application act only on
10 existing species. Results such as those of Robinson et al. (1992), Muys and Lust (1992) and Rundgren
11 (1994), which in some sites did not evidence any increase in earthworm densities following liming,
12 could be explained by the absence of acid-intolerant species in the vicinity of experimental sites. This
13 introduces the problem of the time lapse needed for slow ecological processes such as the adaptation
14 of communities to changing environmental conditions (Burgess 1960). Results from synchronic studies
15 on humus dynamics (Bernier and Ponge 1994) indicated that the course of shifts from moder to mull
16 humus could be conditioned by the activity of some burrowing and acid-tolerant earthworm species
17 such as *Lumbricus terrestris*. Other mull inhabitants may colonize the soil profile only several decades
18 after it has begun to be transformed by this burrowing species. Thus the need for conditions prevailing
19 in mull humus forms, expressed by a lot of saprophagous and even predaceous groups
20 (pseudoscorpions, dolichopodid-empidid and rhagionid larvae), is probably the result of multiple
21 interactions involving feeding, behavioural and physico-chemical requirements of soil animals.

22

23 The action of soil fauna on soil chemical properties is better known, mainly through their building
24 of humus forms (Kubišna 1955; Bal 1970; Hole 1981) and their abovementioned action on nutrient
25 cycling. It has been experimentally verified that the introduction of lacking animal groups, without any
26 further change in environmental conditions, may definitely change site quality (Bal 1982; Scheu and
27 Parkinson 1994). These experiments concerned only the introduction of earthworm species, followed
28 by the appearance of mull humus forms as the result of their burrowing activity. Here we may ask
29 whether the appearance of dysmoder humus form (moder humus with a thick OH horizon) can be
30 determined not only by the absence of zoological groups comprising litter-consuming and burrowing
31 species, but also by high densities of animals such as enchytraeids which we have found in huge

amounts in sites placed on the positive side of axis 1 (Table 3). Enchytraeids have been suspected as having a detrimental influence not only on decomposition of organic matter (Wolters 1988) but also on earthworm populations (Haukka 1987) when they reach high densities. Conversely other authors found them contributing significantly to mineralization processes (Sulkava et al. 1996), thus giving a contrasted landscape concerning the role of these animals in litter decomposition and soil-forming processes.

Beside acidity (water and potassium chloride pH) and C/N ratio, manganese was unexpectedly the only soil nutrient the content of which proved significantly correlated with axis 1. Free and exchangeable acidity and C/N ratio can be considered as involved in feedback loops in the course of humification processes (Ulrich 1986), thus they are as well causes as consequences of the building of humus forms. The manganese content of the topsoil, which is also involved in many biological processes, has been found associated with humus type, together with iron, being much higher in mull than in moder humus (Duchaufour and Rousseau 1959; Toutain and Védry 1975), and is, together with the C/N ratio, highly correlated with vitality of forest trees (Van Straalen et al. 1988). Manganese, as well as iron, oxidizes phenolic acids, thus alleviating allelopathic and complexing processes due to small-molecule aromatic compounds (Lehmann et al. 1987).

If we try to synthesize all these relationships in a common scheme, the following hypothetical sequence can be considered as most realistic, at least in the present stage of our knowledge. Altitude, given the specificity of the studied zone (the Ardenne mountains), can be considered as determining a lot of site features which may drive the soil system towards one or the other of two poles: a mull pole, better expressed in lowland sites, with more animal groups, especially saprophagous macrofauna, and better growth of trees, and a dysmoder pole, better expressed in upland sites, with fewer animal groups, mostly enchytraeids, and poorer growth of trees. Mechanisms of the action of site conditions upon soil fauna (and the reverse) may involve in first the content of leaf litter in metals and alkaline earths, which proved better correlated with faunal abundance and diversity than richness of the soil in these elements. If this hypothesis is true, then mull and dysmoder, stabilized by numerous feed-back loops involving vegetation, decomposers and humus profiles (Perry et al. 1989), should act as steady-state positions for ecological conditions prevailing in beech ecosystems of the Ardenne mountains. In this case the number of intermediate conditions should be less than expected if the sites had been

randomly scaled between these two poles. This may be observed along axis 1, where sites 1, 100 and 28 (mull pole) are clearly isolated from the rest of the sample. Unfortunately the total number of sites of the mull type was not high enough for testing properly the significance of this pattern over the whole range of investigated sites.

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Table 1. Geographical, vegetation and soil features of the 13 investigated sites. AA =Atlantic Ardenne, CEA = Centro-Eastern Ardenne. UA = Upper Ardenne. WA = Western Ardenne. Nomenclature of soil types follows FAO-UNESCO classification (Driessen and Dudal 1991).

Site	Locality	Phytosociological type	Elevation	Soil type
1	Saint-Hubert (CEA)	<i>Luzulo-Fagetum festucetosum</i>	370 m	Dystric cambisol
3	Saint-Hubert (UA)	<i>Luzulo-Fagetum festucetosum</i>	465 m	Dystric cambisol
4	Saint-Hubert (UA)	<i>Luzulo-Fagetum typicum</i>	500 m	Dystric cambisol
5	Saint-Hubert (UA)	<i>Luzulo-Fagetum vacciniotosum</i>	505 m	Dystric cambisol
16	Rienne (WA)	<i>Luzulo-Fagetum vacciniotosum</i>	445 m	Dystric cambisol
17	Rienne (WA)	<i>Luzulo-Fagetum typicum</i>	430 m	Dystric cambisol
22	Haut-Fays (AA)	<i>Luzulo-Fagetum typicum</i>	400 m	Gleyic cambisol
24	Haut-Fays (AA)	<i>Luzulo-Fagetum festucetosum</i>	390 m	Dystric cambisol
26	Willerzie (WA)	<i>Luzulo-Fagetum vacciniotosum</i>	430 m	Leptic podzol
28	Houdremont (WA)	<i>Luzulo-Fagetum festucetosum</i>	375 m	Dystric cambisol
40	Willerzie (WA)	<i>Luzulo-Fagetum vacciniotosum</i>	385 m	Ferric podzol
100	Saint-Hubert (CEA)	<i>Melico-Fagetum festucetosum</i>	350 m	Dystric cambisol
307	Saint-Hubert (CEA)	<i>Luzulo-Fagetum vacciniotosum</i>	380 m	Leptic podzol

Table 2. Coding and methods of recovering used for the different animal groups investigated. MAC = extraction of macrofauna, MES = extraction of mesofauna, MIC = micromorphological dissection. Zoological nomenclature according to Dindal (1990). The methods which have been selected for estimating densities are in bold type.

Code	Animal group	Method of recovering
ANTS	Insecta, Hymenoptera	MES , MIC
CANT	Insecta, Coleoptera, Cantharidae, larvae	MAC , MES, MIC
CATE	Insecta, Lepidoptera, larvae	MAC
CECI	Insecta, Diptera, Cecidomyiidae, larvae	MES, MIC
CENT	Myriapoda, Chilopoda	MAC , MES, MIC
CERA	Insecta, Diptera, Ceratopogonidae, larvae	MAC, MIC
CHEL	Cheliceræ, miscellaneous	MAC
CHIR	Insecta, Diptera, Chironomidae, larvae	MAC, MES, MIC
CLIC	Insecta, Coleoptera, Elateridae, larvae	MAC , MES, MIC
CMIS	Insecta, Coleoptera, miscellaneous, larvae	MAC , MES, MIC
COAD	Insecta, Coleoptera, adults	MAC , MES, MIC
COCH	Insecta, Homoptera	MES, MIC
COLL	Insecta, Collembola	MES , MIC
COPE	Crustacea, Copepoda	MIC
CURC	Insecta, Coleoptera, Curculionidae, larvae	MAC
DERM	Insecta, Dermaptera	MAC
DIPL	Insecta, Diplura	MAC , MES, MIC
DMIS	Insecta, Diptera, miscellaneous, larvae	MAC, MES, MIC
DOEM	Insecta, Diptera, Dolichopodidae + Empididae, larvae	MAC, MES , MIC
ENCH	Annelida, Oligochaeta, Enchytraeidae	MES, MIC
FANN	Insecta, Diptera, Muscidae, larvae	MAC
ISOP	Crustacea, Isopoda	MAC , MES, MIC
LIMN	Insecta, Coleoptera, Limnobiidae, larvae	MAC
LMIS	Insecta, miscellaneous, larvae	MAC
LUMB	Annelida, Oligochaeta, Lumbricidae	MAC, special extraction
MILL	Myriapoda, Diplopoda	MAC , MIC
MITE	Acari, excl. Oribatida	MES, MIC
MOLL	Mollusca, Gastropoda	MAC , MIC
OPIL	Cheliceræ, Phalangida	MAC
ORIB	Acari, Oribatida, miscellaneous	MES , MIC
PAUR	Myriapoda, Pauropoda	MES, MIC
PHTH	Acari, Oribatida, Phthiracaridae + Euphthiracaridae	MES, MIC
PROT	Insecta, Protura	MES, MIC
PSEU	Cheliceræ, Pseudoscorpionida	MAC , MES, MIC
PSOC	Insecta, Psocoptera	MES, MIC
PSYC	Insecta, Diptera, Psychodidae, larvae	MAC
RHAG	Insecta, Coleoptera, Rhagionidae	MAC
SCAT	Insecta, Diptera, Scatopsidae, larvae	MAC
SCIA	Insecta, Diptera, Sciaridae, larvae	MAC, MIC
SPID	Cheliceræ, Araneida	MAC , MES
SYMP	Myriapoda, Symphyla	MES, MIC
THRI	Insecta, Thysanoptera	MES , MIC
TIPU	Insecta, Diptera, Tipulidae, larvae	MAC , MIC
TRIC	Insecta, Trichoptera, larvae	MAC

PONGE

Table 3. Mean densities.m⁻² of zoological groups in the 13 investigated sites, ordinated according to axis 1 of correspondence analysis.

	100	1	28	3	22	24	17	16	307	5	40	26	4
LIMN	17	21	6.3	0.5	2.5		0.5		0.8				
SCAT	1.6	3.1	0.9	0.5		0.5							
DOEM	1200	160	780	160	26	160	100	100	34	28	3.7	5.2	5.2
MILL	54	24	16		2.2						2.9	2	
TRIC	0.9	1.6											
CANT	0.7	3.3	5.2	0.5	0.9		0.5	0.5			0.5		
ISOP	42	0.5	2		0.5						0.5		
LUMB	61	2	0.5	1.3					1.6				
PSEU	17	20	25	10	8.3	4.8	6.7	12	9.5	8.8	3.8	0.7	8.2
RHAG	6.6	24	44	12	16	12	6	8.8	1.7	7.3	5.5	0.7	1.3
CHIR	800	570	980	2500	690	19	44	65	19	1100		34	
MOLL	6			0.5			0.5						
FANN	1.3	1.3	14		0.5	0.5	0.5				1.6	0.7	
CENT	100	99	160	63	21	7.8	69	55	20	12	98	54	16
OPIL		0.5	0.5				0.5						
CHEL		5.6				0.7			0.5				
CERA			400										
TIPU	2.2	0.9	0.5	2.5	2.5	0.5	0.5		0.7	1.6	1.6		0.5
PROT			1500		19	19							
PAUR	19		5400		27	27		44	2400				
CECI	800	400	48		570	27	1300		1100	27	1700	19	19
CMIS	34	30	47	37	23	43	32	14	29	39	39	34	25
DERM			1.3										0.7
SPID	11	8.6	8.7	53	9.4	2.9	4.8	8	19	2.3	5.5	13	10
LMIS		0.5										0.5	
SCIA	1500	1700	5800	1700	65	1800	3700	3900	2000	19	17000	980	4200
ORIB	55000	150000	110000	80000	43000	44000	62000	94000	210000	87000	72000	100000	57000
COAD	15	8.9	11	27	5.5	22	4.4	13	9.3	18	17	10	9.6
COPE			19						19				19
ANTS						28							
DMIS	19	19				27		19			27	19	39
THRI		21	4.6		3.7		21		26		3.7	3.7	21
PSYC										1.1			
PSOC												27	
CATE		0.5								0.8		0.5	0.5
MITE	13000	18000	33000	32000	19000	11000	24000	38000	32000	14000	29000	29000	28000
CURC													0.5
COLL	42000	70000	59000	88000	38000	51000	57000	71000	100000	68000	45000	81000	120000
COCH									27		19	34	
PHTH	2900	8200	20000	7300	29000	5100	43000	24000	33000	15000	27000	9600	16000
SYMP		400		19		19	980	39	27	1100	570	19	
DIPL	15	0.7	97	2.9	23	38	87	21	25	36	98	140	50
CLIC	3.1	6.7	41	81	38	6.4	12	20	18	130	120	84	39
ENCH		12000	89000	100000	150000	180000	170000	46000	130000	79000	400000	410000	380000 800000

Table 4. Vegetation and soil features of the 13 investigated sites, ordinated according to axis 1 of correspondence analysis.

	100	1	28	3	22	24	17	16	307	5	40	26	4
Elevation (m)	350	370	375	465	400	390	430	445	380	505	385	430	500
Phytosociological type:													
Melico-Fagetum festucetosum	+												
Luzulo-Fagetum festucetosum		+	+	+		+							
Luzulo-Fagetum typicum					+		+		+	+	+	+	+
Luzulo-Fagetum vaccinietosum								+	+	+	+	+	
Soil type:													
Dystric cambisol	+	+	+	+		+	+	+		+			+
Gleyic cambisol					+								
Leptic podzol									+			+	
Ferric podzol											+		
Humus form:													
Oligomull	+												
Dysmull	+	+				+							
Amphimull			+						+				
Hemimoder							+						
Eumoder			+	+	+		+	+		+			
Dysmoder					+	+				+	+	+	+
Height of trees (m)	37	42	38	36	36	39	37	37	26	37	24	31	35
Litter accumulation index (LAI)	1.1	3.1	14.1	9.8	10.4	7.3	6.0	9.1	10.3	8.7	9.0	9.4	7.2
OF+OH (kg.m ⁻²)	0.8	2.3	9.0	8.7	6.9	4.3	4.8	5.7	8.4	5.9	7.7	7.7	6.6
Soil analyses (A horizon):													
pH water	4.3	3.8	3.6	3.6	3.7	3.6	3.4	3.3	3.6	3.5	3.1	3.4	3.6
pH KCl	3.6	3.1	3.0	2.8	3.1	3.0	2.7	2.6	2.8	2.9	2.0	2.5	2.9
C/N	14.5	14.2	14.9	16.6	16.5	16.6	18.3	18.9	19.5	17.4	19.8	18.9	17.8
Total Ca (%)	0.19	0.11	0.02	0.03	0.05	0.04	0.10	0.09	0.02	0.11	0.06	0.04	0.02
Total Mg (%)	0.12	0.10	1.17	0.11	0.24	0.18	0.11	0.11	0.11	0.13	0.04	0.11	0.19
Total K (%)	0.25	0.21	0.21	0.25	0.24	0.25	0.23	0.24	0.30	0.26	0.13	0.23	0.28
Total Na (%)	0.08	0.11	0.06	0.11	0.07	0.09	0.11	0.19	0.07	0.12	0.05	0.08	0.10
Total iron (%)	8.0	8.6	10.2	9.1	4.9	5.4	4.6	5.5	7.9	9.4	1.4	4.8	6.9
Total manganese (%)	0.24	0.16	0.15	0.11	0.04	0.08	0.02	0.01	0.11	0.07	0.00	0.01	0.04
CEC (meq.100g ⁻¹)	13.1	7.5	11.1	10.6	10.2	10.6	15.2	16.1	8.6	9.1	21.4	15.0	13.0
Exchangeable Ca (meq.100g ⁻¹)	3.48	0.25	0.29	0.72	0.22	0.14	0.98	0.26	0.11	0.09	0.86	0.36	0.30
Exchangeable Mg (meq.100g ⁻¹)	0.61	0.17	0.33	0.21	0.16	0.15	0.39	0.29	0.25	0.13	0.69	0.30	0.29
Exchangeable K (meq.100g ⁻¹)	0.44	0.25	0.23	0.34	0.29	0.24	0.46	0.31	0.31	0.18	0.57	0.35	0.32
Exchangeable Na (meq.100g ⁻¹)	0.13	0.07	0.08	0.06	0.05	0.07	0.10	0.12	0.11	0.08	0.19	0.14	0.10
Litter analyses:													
Ashes in total litter (%)	6.7	5.4	3.9	3.7	4.2	4.0	3.6	3.1	4.2	2.9	3.7	2.7	3.2
N in total litter (%)	1.4	1.6	1.6	1.7	1.5	1.5	2.0	1.4	1.1	1.4	1.7	1.5	2.2
C/N in total litter	31.9	24.3	30.5	31.0	32.4	36.7	27.4	32.4	44.7	36.4	29.5	36.0	24.0
Ca in total litter (%)	1.22	0.60	0.52	0.44	0.42	0.45	0.44	0.37	0.50	0.39	0.55	0.37	0.42
Mg in total litter (%)	0.14	0.06	0.08	0.04	0.05	0.05	0.06	0.05	0.07	0.05	0.08	0.05	0.06
K in total litter (%)	0.32	0.31	0.21	0.32	0.27	0.30	0.52	0.26	0.34	0.33	0.42	0.31	0.31
Fe in total litter (mg.kg ⁻¹)	930	1100	540	390	610	520	540	440	560	310	330	220	350
Ashes in beech leaf litter (%)	8.2	5.0	4.3	4.5	4.7	4.7	4.0	3.3	4.4	3.2	4.1	3.3	3.8
N in beech leaf litter (%)	1.4	1.6	1.6	1.7	1.5	1.5	2.0	1.4	1.1	1.4	1.8	1.6	1.5
C/N in beech leaf litter (%)	29.8	27.6	29.8	26.2	30.1	31.5	23.3	31.8	38.9	34.1	25.5	30.5	29.8
Ca in beech leaf litter (%)	1.84	0.72	0.62	0.56	0.58	0.60	0.50	0.41	0.68	0.51	0.63	0.46	0.54
Mg in beech leaf litter (%)	0.18	0.05	0.08	0.04	0.04	0.04	0.05	0.04	0.07	0.04	0.07	0.05	0.05
K in beech leaf litter (%)	0.22	0.2	0.14	0.21	0.14	0.18	0.36	0.15	0.22	0.19	0.39	0.25	0.18
Fe in total litter (mg.kg ⁻¹)	730	640	540	470	430	530	530	420	410	330	310	250	360

Legends of figures

Fig. 1. Ordination of sites (13) and zoological groups (44), used as main variates, according to their coordinates along axis 1 of correspondence analysis. Coding of sites and zoological groups according to Tables 1 and 2, respectively. The position of the origin is indicated by an arrow. Codes for zoological groups belonging to macrofauna are in bold type. Variates significantly correlated with axis 1 coordinates were indicated by rectangular bordering.

Fig. 2. Ordination of sites (13) and some additional variates (elevation, humus forms, soil types, phytosociological types), according to their coordinates along axis 1 of correspondence analysis. Variates significantly correlated with axis 1 coordinates were indicated by rectangular bordering.

Fig. 3. Ordination of sites (13) and some additional variates (pH and C/N ratio in the A horizon, litter accumulation, height of trees) according to their coordinates along axis 1 of correspondence analysis. Variates significantly correlated with axis 1 coordinates were indicated by rectangular bordering.

Fig. 4. Ordination of sites (13) and some additional variates (exchangeable and total bases in the A horizon) according to their coordinates along axis 1 of correspondence analysis. Variates significantly correlated with axis 1 coordinates were indicated by rectangular bordering. Plus or minus sign means higher or lower values, respectively.

Fig. 5. Ordination of sites (13) and some additional variates (mineral content of litter) according to their coordinates along axis 1 of correspondence analysis. Variates significantly correlated with axis 1 coordinates were indicated by rectangular bordering. Plus or minus sign means higher or lower values, respectively.

PONGE

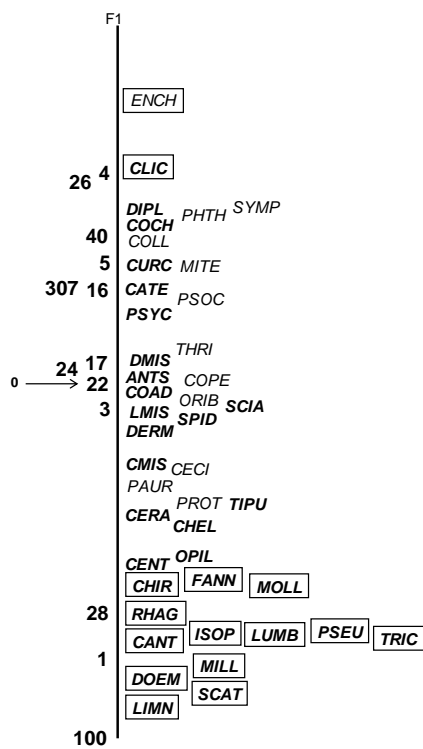


Fig. 1

PONGE

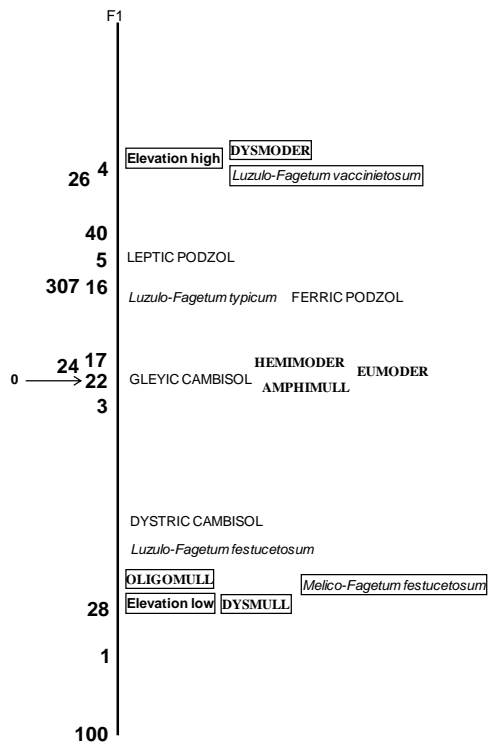


Fig. 2

PONGE

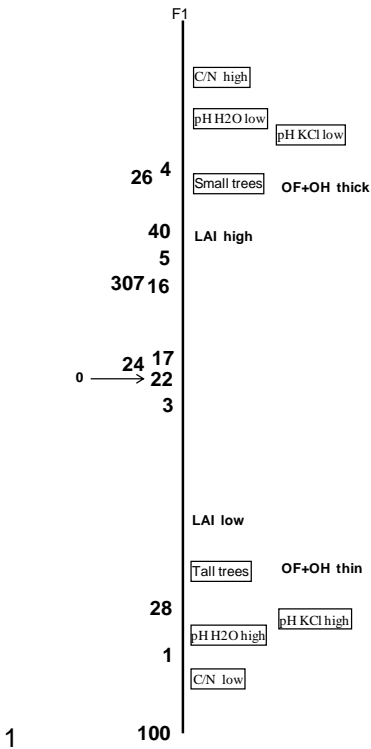


Fig. 3

PONGE

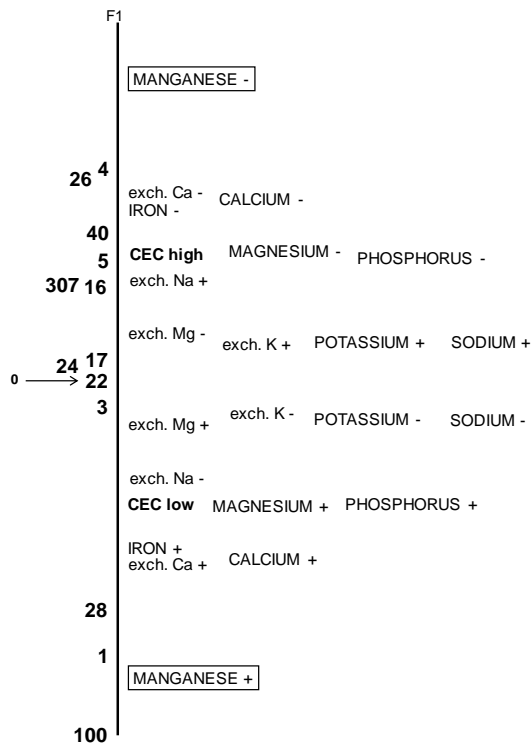
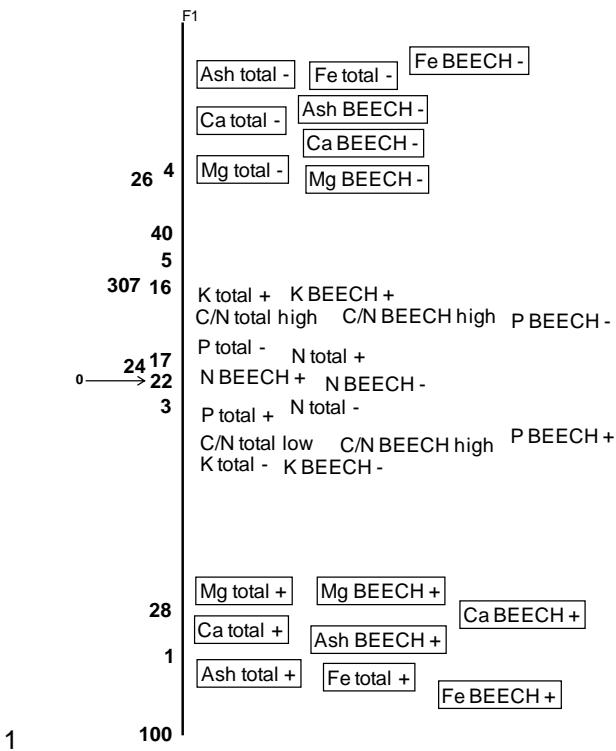


Fig. 4



2 Fig. 5